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THE FEEDING HABITS AND FOOD OF PELAGIC COPEPODS AND THE QUESTION OF NUTRITION BY ORGANIC SUBSTANCES IN SOLUTION IN THE WATER

BY

CALVIN O. ESTERLY

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It is well known how some of the animals that feed on the minute organisms of the plankton obtain their food. For example, the particles ingested by the appendicularians are gathered by means of a screen-like arrangement that separates them from a current of water. Or, as in the case of the Salps, the food material is entangled in mucus and then carried to the opening of the esophagus.

The matter is different, however, when such forms as the Copepoda are considered. These animals are provided with well-developed appendages which have a varied equipment of bristles. The copepods feed upon the minute animals and plants of the plankton (Peck, 1896; Dakin, 1908), and it is a rather interesting question how the complex appendages are used in getting food. Such organisms as diatoms are too small to be grasped or manipulated by the bristles of the mouth parts, yet the copepods ingest diatoms in large numbers.

The literature, so far as I have been able to discover, contains no accurate information as to the method by which the pelagic copepods get their food. Dakin (1908, p. 776) speaks of "the food-matter caught by the mouth appendages and introduced into the mouth by the mandibles," but he does not say much more about the process. Lohmann (1911, p. 11) states casually that a large part of the copepods make the same filtration experiment as the appendicularians,

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but he does not tell how the filtering is accomplished or what organs take part.

The method of food-getting by the Ostracoda appears to have received more attention, and since it is similar to that in the copepods, it may be well to make note of it here. Biedermann (1911, p. 651) gives this account for the Daphnids:

> Die betreffenden Körperchen werden durch Bewegungen der Beinanhänge herbeigestrudelt und schlieslich zu einem Bissen geformt, der dann durch peristaltische Bewegungen des Oesophagus rasch in den Mitteldarm befördert wird. Mittels der reusenartigen Fortsätze ihrer beständig auf und ab bewegten Gliedmassen vermögen die Daphnien grosse Wassermengen durchzuseihen.

Woltereck (1908, p. 872) makes very similar statements.

I can state, from observations upon *Calanus finmarchicus* and *Eucalanus elongatus,* that the copepods get their food in essentially the same manner as the ostracods. I have watched many living specimens of *Calanus* get carmine grains in what appears to be necessarily the method by which they obtain organisms for food from the sea water.

When a living *Calanus* is put into a small amount of water, the animal nearly always scurries about, ventral side up. Under these conditions it is possible to see how solid particles are concentrated and taken into the mouth. The necessary preliminary to actual ingestion is the production of currents which transport the particles toward the body. The movement of the water is due to the activity of the appendages, chiefly those of the head. It is not possible to state just how the currents are set up, because of the great rapidity with which the appendages move. It is easy to determine that the bits of carmine are brought from considerable distances toward the body; they come from in front of the animal and pass between the bases of the anterior antennae, or from behind the bases of the posterior maxillipeds. In both cases the particles are driven toward the mouth. At times, however, the carmine is driven in all directions from the body, but one cannot see how this is brought about.

While some of the appendages play an active part in the process of food-getting, others with their bristles assume a passive but important role. This consists in directing the moving particles definitely toward the mouth, and it is brought about chiefly by the long spinose bristles of the anterior maxillipeds. As indicated in figure 1, they are so arranged that those of each appendage form the side of a trough or funnel which narrows at the anterior end. The long bristles do not

fit closely together, but the spaces between them are reduced by the interlacing spinules, or "cilia." The spinules all point toward the tip of the bristles so that the progress of solid particles along the bristles

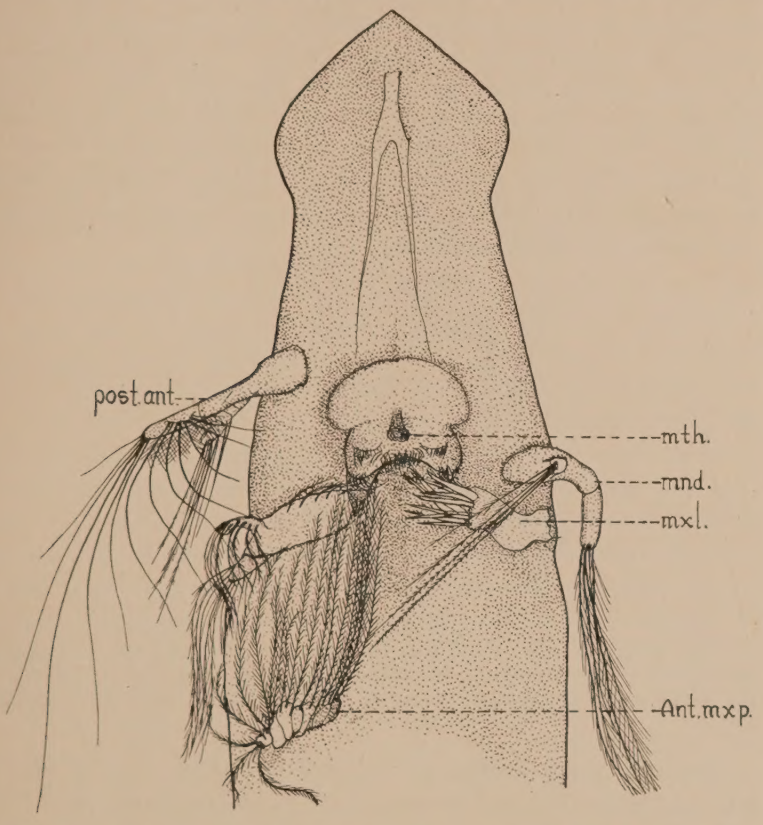

Fig. 1. A view, from below, of the mouth region of *Eucalanus*. The appendages and bristles are shown partly diagrammatic. On the left of the figure are shown, from behind forward, the anterior maxilliped (*ant. mxp.*), the outer lobe of the maxilla, the posterior antenna (*post. ant.*); on the right appear the inner lobe of the maxilla (*mxl.*) with stiff, heavy bristles and the rami of the mandible (*mnd.*), the "jaw" being omitted. The shield-shaped prominence in the center of the figure bears the scoop-like lip, within which is the opening of the mouth (*mth.*). The side of the funnel formed by the bristles of the anterior maxilliped is shown on the left of the figure, the other side being omitted for the sake of clearness.

is not retarded. The grains of ink or carmine strike the sides of the funnel and are carried along until they reach its apex, where they are formed into a little ball or pellet.

The mouth opening (figs. 1, 2, *mth.*) lies anterior and dorsal to the margin of a prominent scoop-shaped lip (fig. 2), and the tips of the long bristles that form the sides of the trough reach beyond the lateral margins of the scoop so that the anterior end of the funnel is completed on the ventral side by the lip (fig. 1). The cluster of grains is held immediately behind the mouth, in the pocket formed by the ventral and lateral portions of the lip and the wall of the body dorsally. The pellet is taken through the mouth into the gut when the upper end of the esophagus is widened by the action of dilator muscles, as noted by Dakin (1908, p. 776), and when in the stomach it is carried back and forth by peristalsis.

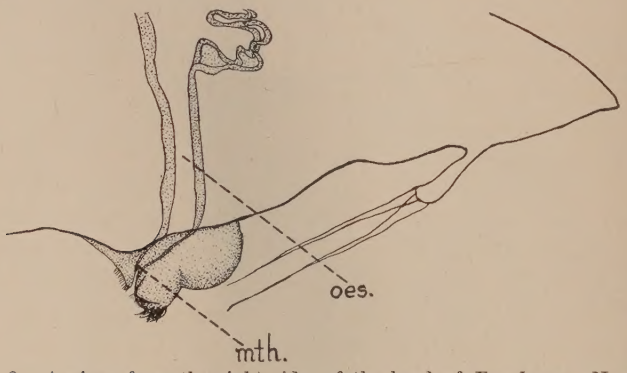

Fig. 2. A view, from the right side, of the head of *Eucalanus*. No appendages are shown; the prominent lip appears beneath the head, and the opening of the mouth (*mth.*) is indicated (above the lip) from which leads the oesophagus (*oes.*).

The stiff, heavy bristles on the inner lobe of the maxilla (fig. 1, *mxl.*), are used to crowd the mass more closely under the lip. They do not move very often, but it is not difficult to determine what their part is. They act much like fingers in keeping the pellet in position.

After the pellet has been formed and held in position, it often happens that it is broken up and the particles are scattered widely. This is accomplished by a backward sweep of the bristles in the sides of the trough, aided to some extent by a movement of the bristles on the inner lobe of the maxilla in the same direction. I have not observed that the anterior maxillipeds make any other movements than those that lead to the dispersal of the pellet. I have not been able to determine what the jaws of the mandibles do, though it seems probable that they are used to break up objects that are too large to be taken through the mouth.

It seems clear that the free-swimming copepods must obtain their food in the general way set down above, but some individuals will not ingest particles of carmine under the conditions that others do. All the animals in a watch-glass are in constant activity with the characteristic jerky movements, but not all of them will show the carmine in the digestive tract. This suggests that the movements of the appendages that lead to locomotion are not necessarily the ones that cause solid particles to gather in the mouth region. There may be special movements of certain appendages or of parts of them that cause the pellets to form. There is a possibility, however, that the pellets are constantly formed and as regularly rejected by the animals that do not take in the carmine.

The formation and ingestion of the particles takes place rapidly. If specimens of *Calanus* are taken from clean water and put into a watch-glass at the edge of the stage of the microscope and carmine is added, the coloring matter will have been ingested within the few seconds that elapse before the animals can be brought under the objective, and the particles can then be seen as they move back and forth in the digestive tract. On the other hand, specimens have been kept in good condition for three or four hours in water containing carmine, and in that time most of the animals did not show the color in the tube. Attention may be called to the similarity between the process of food-getting just described for the Copepoda, and that in *Paramecium,* where the oral groove and cilia take the place of the bristles and complex appendages.

While I have observed the actual ingestion of solid particles only in *Calanus,* I have often seen the pellets formed by *Eucalanus,* but they were not taken into the mouth. The figures shown are of *Eucalanus,* but the structures are so similar in *Calanus* that the one will do for the other. The essential occurrences are the same in both these forms, so far as I have been able to determine, though there are certain structural differences in the appendages.

The question of how marine animals are nourished has caused a good deal of discussion within the last few years. This seems to have been brought about largely by the introduction of Pütter's ideas. This investigator (Pütter, 1907 *a, b,* 1909), as is well known, believes there is evidence that the food requirements of many forms can not be met if the animals are dependent on organic material actually ingested. If this is true, there is some other source of utilisable food, and it is found, according to Pütter, in the organic compounds in solution in

the water. Pütter (1909, p. 4 ff.) gives figures which, he states, indicate the amount of food needed by various forms, and he shows (1909, pp. 105–107) that there is a much larger quantity of soluble organic compounds in a volume of water than there is of solid food as found in the plankton organisms. He shows, furthermore (1909, p. 49), that to satisfy the food requirements by the ingestion of plankton organisms, it would be necessary for an animal to filter an unbelievably large volume of water if the volume of the animal itself is considered. It follows, therefore, that the substances in solution, though but slightly concentrated, form an additional source of food, and Pütter (1909, pp. 44–53) gives instances to show that such substances really are used. His general conclusion is as follows (1909, p. 147):

> Die Ernährung eines grossen Teiles der Formen aller Stämme vollzieht sich nicht in der Weise, wie man bisher, in grober Analogie mit den Säugetieren und Vögeln annahm; d. h. dass geformte Nahrung aufgenommen, durch die Verdauung gelöst und gespalten und in diesem Zustande resorbiert wird, sondern eine grosse Anzahl von Tieren, speziell die absolut kleinen Formen aller Stämme, nehmen, so weit sie im Wasser leben, ihre Nahrung direkt in gelöster Form aus dem Wasser.

This view was apparently retained in 1913 (Pütter, 1913).

While Pütter's presentation of data is impressive, his contention as to dissolved food substances is not supported by subsequent investigation. The recent studies of Moore, Edie, Whiteley and Dakin (1912, 1913) led them to agree with Pütter so far as to say that *uniformly distributed* plankton is not sufficient to maintain nutritive equilibrium. These investigators found (Moore *et al.*, 1912, pp. 260, 281) that the organic material contained in the plankton obtained by passage through a no. 20 net and a Chamberland filter is, on the average, one part in a million. Under such conditions, only forms with slow metabolism (such as sponges or ascidians) can possibly be nourished upon the plankton. Pütter's results as to the amount of dissolved organic compounds are not confirmed, however, and Moore and his co-workers attribute his high figures to faulty methods of analysis, their results (p. 280) being that the soluble material does not exceed one part in a million. Pütter (1909, p. 145) gives 10 to 20 mg. per litre as a rough estimate of the average content of sea water in dissolved organic compounds.

The answer of Moore and the others (1912, p. 260) to the question, What is the food supply, then? is that it is the plankton but only when it occurs in rich shoals; that is, the swimming plankton feeders must seek the best grounds in order to get enough food to maintain nutritive equilibrium.

It must be kept in mind, however, that there are large quantities of plankton consisting of organisms so small that the finest nets do not capture them. This is the so-called nanno- or centrifuge plankton of Lohmann (1911), and Lohmann believes that organisms like these comprise most of the food of such forms as the microcrustacea and the appendicularians. Unless special methods of collecting are employed, this part of the plankton will be neglected in an estimate of the amount of food available.

This paper is not intended as a review or criticism of Pütter's work, although it must necessarily be mentioned. One way of answering in a measure the questions he raises, as he himself suggests (Pütter 1909, p. 51), is by determining, through an examination of the contents of the intestine, what organisms and how many of them are eaten by the plankton feeders.

The important group of the Copepoda has been examined in this way by Dakin (1908), who studied the contents of the gut in several species. He found that diatoms are the most abundant organisms in the tract, especially specimens of *Thalassiosira* or *Coscinodiscus* so small that they would pass through a no. 20 net. *Peridinium divergens* and *P. cerasus* were next in frequency. Silico-flagellates did not occur in large numbers, the Tintinnidae were rare and *Ceratium* appeared to be absent (Dakin, 1908, pp. 777–779). Dakin noted that in many cases the tract was full of a green mass, as Hensen (1893, p. 94) had found, and the former states (Dakin, 1908, p. 777) that, in his opinion "it is the micro-organisms, many of which pass through even a no. 20 'Müllergaze' that play the most important role."

So far as I am aware, Dakin's paper is the only one that deals especially with the food of marine copepods. Hensen (1893, p. 94) states that repeated searching revealed only one shell of a *Cyclotella,* although the tract was always full of a green mass which he regarded as derived from diatoms.

I have recently examined the intestinal contents of several hundred copepods of different species, taken at different seasons and at different depths. All had been preserved in formalin. The animals were divided with a scalpel into right and left parts, the section being a little to one side of the middle line. The entire digestive tract was removed by means of a needle, and mounted by itself in glycerine. Such preparations are very easy to make, and can be examined with the oil-immersion.

Most of the specimens examined belonged to *Calanus finmarchicus* and the facts about the intestinal contents of that form, as I found them, are as follows. It happens that in a third of the cases the tube had no contents at all. Practically all of the other specimens, however, showed a green or greenish-yellow mass of varying extent. In some it filled the intestine, in others there was only a small bit, but the characteristic color was present. The colored mass, even under the oil-immersion, was homogeneous, except for broken bits of diatom shell and particles of detritus and mineral matter.

The recognisable remains of organisms in the gut of *Calanus* consist chiefly of the shells of diatoms, of which *Coscinodiscus* is the most abundant. Broken or entire shells occur in most cases when diatoms are present at all. It is hard to estimate the number of specimens when the shells are broken; I saw one or two entire tests, and fragments are more abundant. In three cases there were masses of broken *Coscinodiscus* shells, and evidently the plants had been ingested in large numbers. Usually, however, the number of pieces, even, is under ten. Another diatom that occurred frequently was one of the *Thalassiothrix* type, but the shells were not found as often as those of *Coscinodiscus*. In several instances the intestine was packed full of pieces of *Thalassiothrix*. The diatoms *Planktoniella* and *Navicula* occurred, also, the former in one copepod and the latter in two.

Eleven specimens of *Calanus* contained fragments of a silicoflagellate closely resembling *Dictyocha* (if not that form) but not over four of the pieces were seen in one animal.

It is interesting to find that *Calanus* ingests the Coccolithophores. Gran (1902, p. 163) observed the plates in the fecal capsules of copepods, and Murray and Hjort (1912, p. 382, 719) also mention that the plates occur in the capsules. Nineteen specimens of *Calanus* that I examined had the coccoliths in the intestinal contents. The numbers varied widely; in some the intestine was literally packed with them, but usually there were not many. There were twenty entire organisms in one copepod, nine in another. The coccolithophores belong almost entirely to that group which has the perforated coccoliths (Lohmann, 1902, p. 127), but I saw two with the rodlike coccoliths. The one commonly found is much like the drawing of *Pontosphaera huxleyi* as shown in plate 4, figure 3, of Lohmann's paper (1902).

Other organisms were found to occur in the gut of *Calanus*. A species of *Dinophysis* was found in five specimens, one of which contained two of the cells. *Prorocentrum* (probably *P. micans*) was

found in seven specimens, one of which contained 63 of the protozoans and another twelve; the intestine in the former case was closely packed with the cells. *Peridinium* was recognised in seven, two of them in one copepod; in this particular case the cells had retained their shape but were without contents, while in the others the tests were wrinkled and distorted yet recognisable as those of some *Peridinium*. Mangin (1911, p. 45) has noted the effect of the digestive processes of various animals on *Peridinium*. One *Calanus* contained the skeleton of a nauplius, and in three instances there were the broken bristles of some crustacean.

Eucalanus elongatus.—This copepod is abundant in the San Diego region, ranking next to *Calanus*. *Eucalanus* is exceedingly transparent, so that the entire digestive tract can be seen through the exoskeleton and muscles. I have examined numbers of this copepod both living and in serial sections, and have never seen the recognisable remains of any ingested organism. Most specimens, in fact, are devoid of any intestinal contents, though in two cases I have seen a fecal capsule in the posterior part of the tract; the capsule, however, contained only a colorless granular mass of homogeneous character.

Scolecithrix persecans.—This copepod is notable because in all of the seventeen specimens the intestinal contents were abundant. All of the animals contained crustacean bristles, and in some instances the gut was packed with them. Many of the bristles were those of some copepod, but it is certain that there were the remains of other crustacea. The tract of several specimens were filled with a red-brown mass of finely granular material in which the bristles were contained. Two specimens of this copepod had ingested *Coscinodiscus* in small numbers.

Pleuromamma quadrungulata.—Fifteen specimens were examined. In six the tract was empty except for a few scattered mineral particles. Of the others, one contained a piece of a radiolarian test, three had broken bristles of some sort, and five showed traces of the greenish material.

Pleuromamma abdominalis.—Out of fifteen specimens, there were seven whose intestinal tracts were empty, while six had more or less of the green color. Among the organisms recognised were the diatoms *Synedra, Thallasiothrix, Fragilaria* and *Coscinodiscus,* all as fragments; *Dictyocha; Globigerina;* broken bristles of a copepod. In no case was the tract even moderately full.

Gaidius pungens.—Sixteen were examined, and only two of them were entirely empty. Eight showed the green color. The organic remains consisted of broken *Coscinodiscus, Dictyocha* and a radiolarian; in addition nine of the animals contained broken bristles, but I could not determine their source. On the whole, judging from these specimens, this copepod may be said to get an abundance of food.

Undeuchaeta bispinosa.—Six of the twelve specimens had nothing in the tract; four of the others showed a bit of green material, one contained several copepod feet, and the remaining one had a *Chaetoceras* bristle and a large amount of stuff with the appearance of mineral debris.

Since the copepods form an important group because of their numbers in the plankton and because they are used as food by higher organisms (Peck, 1896, p. 353), the food of the copepods is of more than incidental interest. It seems plain enough that the copepods feed principally upon the small forms of the plankton, such as the diatoms, so far as one can judge from an examination of the intestinal contents. But, as has been pointed out by Lohmann (1909), and Biedermann (1911, pp. 650, 651), this method involves a certain amount of error, which may be considerable. Only the indigestible portions of the food can be recognised, and it is certain that forms are ingested which do not have shells or skeletons. To determine accurately what is eaten and how much, it is necessary to be able to observe the animals alive and while feeding (Lohmann, 1909, p. 26). This would permit one to determine how much food material passes through the gut in a given time, which, as Biedermann has pointed out (1911, p. 650), it is more important to ascertain than to estimate from the intestinal remains how much was eaten.

It is interesting to note, however, that many of the intestinal canals examined were devoid of contents. We may reasonably assume, under such conditions, that food either has not recently been ingested or that it consists of exceedingly delicate forms that are soon broken up without leaving traces. The amount of material in the intestine ought to furnish some clue as to the amount of food eaten. The specimens of *Gaidius* and of *Scolecithrix persecans* which I saw appeared to have had an abundance, but only one *Calanus* could be said to be in that condition and it had over sixty cells of *Prorocentrum*. *Eucalanus* never has solid contents in the tracts so far as my observation goes.

With these matters before us, it is interesting to consider the figures given by Pütter (1909, p. 63) as to the needs of a *Calanus*.

He has estimated that a "*Calanus* spec." will require 15,800 *Coscinodiscus* of medium size daily, or 9,750,000 *Thalassiosira nana,* to cover its food needs. If these figures are even approximately correct, it must be evident that the needs of a *Calanus* in the San Diego region are either far from satisfied or else there is some other source of food than that which appears in the intestinal contents. Dakin (1908, p. 777) counted 200 diatoms as a maximum number, while many animals did not have anything in the alimentary canal, and in a review of Pütter's work (Dakin, 1910, p. 214) he states that if the figures given by Pütter for the food requirements of copepods are correct, he does not see how they get enough food in diatoms or flagellates. He will be ready to accept, then, Pütter's theory that dissolved substances form an additional source of food.

If the unicellular plants and animals comprising the centrifuge plankton are taken in large enough numbers, the problem is solved so far as the copepod is concerned, and such organisms will not leave definite traces. But if the green matter noted so often is derived from such food organisms, they are not taken in large numbers in these waters, if one may judge from the amount of that material that shows in the tracts of animals preserved in formalin.

Although the part taken by the centrifuge plankton in the nutrition of the marine copepods is not known, it is probable that those unicellular forms are most important, and that the ingested numbers could be ascertained from a study of living copepod material. Lohmann (1909, p. 24) states that the forms of the nannoplankton like chrysomonads or *Rhodomonas* can be recognised in living Tintinnidae or naked ciliates, while in preserved material only the skeletons of silico-flagellates and diatoms or the remnants of *Peridinium* can be seen. The same may be true of the intestinal contents of the copepods. As things are, it is largely a matter of opinion what forms other than those with skeletons are present.

In the case of some of the fresh-water Cladocera, however, Woltereck (1908) showed that the centrifuge plankton has an important role. He found that these crustaceans are better nourished in the upper lake at Lunz than in the lower lake, though the net-plankton is much greater in the latter. The upper lake, however, contains a richer centrifuge plankton, and these are the organisms that are regarded as of first importance in the nutrition of the Cladocera.

The answer to the important questions raised by Pütter's investigations will be most readily obtained, probably, by ascertaining what

organisms are used as food and in what numbers. If we can discover how much food is taken by *Calanus,* even as a very rough average from a large series of observations, we shall have to be satisfied that the food requirements are met, whether the actual results conform to the theoretical needs or not.

SUMMARY

1. Particles that float (such as grains of carmine) are carried toward the mouth by water currents set up by movements of the head appendages. The particles are definitely directed by means of the sides of a sort of trough formed by the long bristles of the anterior maxilliped. These appendages are stationary most of the time.

2. There is formed a little pellet, which is held immediately behind the mouth and then taken in when the esophagus is dilated.

3. It appears that the ordinary movements of locomotion are not necessarily those that cause the formation of the pellets, since animals may be kept for hours in water to which carmine has been added without ingesting the particles, while in other cases the color appears in the intestinal tract in a few seconds.

4. An examination of the digestive tracts of several species of marine copepods shows that diatoms are the organisms whose remains appear most often, but in many cases the tracts are empty or contain only bits of debris and more or less of a green mass.

5. The amount of food that is indicated by the intestinal contents is surprisingly small in the majority of cases, and especially so when the figures given by Pütter as to the needs of a copepod are considered.

6. It is likely, however, that the food of these animals consists to an important degree of organisms of the centrifuge plankton which are without shells and do not leave recognisable remains. At any rate, this possibility needs careful investigation before Pütter's theory of nutrition through dissolved organic material is accepted.

Transmitted December 27, 1915.

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